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Hawaiian Winter Workshop [12th] Held in the University of Hawaii at
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Brownian bugs and superprocesses

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Abstract. Advection-diffusion-reaction (ADR) models link physical oceanography and biological oceanography. These models, which describe biology using continuous concentration fields, usually neglect individual-scale fluctuations. I describe a stochastic individual-based model, called the Brownian bug process, which illustrates some of the surprising issues associated with the neglect of fluctuations by ADR descriptions. The Brownian bug model is an ensemble of random walkers which suffer birth and death at constant mean rates. (Probabilists will recognize the Brownian bug model as the simplest example of a "superprocess.") Binary division puts two bugs (parent and progeny) at the same position and the accumulation of these small-scale density fluctuations can produce palpable nonuniformities on large scales. In other words, provided that the diffusion is not too strong relative to the reproduction rate, a spatially homogeneous initial condition spontaneously develops patches and voids. The wavenumber signature of these reproductive pair correlations is that the spectrum of density fluctuations remains white but rises linearly with time. Diffusion opposes this reproductive forcing, most effectively at large wavenumbers, so that a red spectrum develops.

1. Introduction

Individuals are the fundamental unit of ecology but it is not feasible to model ecological processes by tracking single organisms. Instead, ecologists often employ advection-diffusion-reaction (ADR) approximations which describe biology using the 'concentration' $C(\mathbf{x}, t)$ (e.g., *Flierl et al.* 1999). The concentration is defined via a sample area¹ dA surrounding any \mathbf{x} at time t :

$$C(\mathbf{x}, t) dA = \text{expected number of organisms in } dA. \quad (1)$$

The dimensions of dA are such that the strong nonuniformities characteristic of scales comparable to that of an individual are greatly reduced by averaging.

Ecological ADR models originated with papers by *Fisher* (1937), *Kolmogorov et al.* (1937) and *Skellam* (1951). These authors independently proposed

$$C_t = \gamma C - \lambda C^2 + D \nabla^2 C \quad (2)$$

as a model for the growth, saturation and dispersion of a population. This chapter of theoretical ecology is either a slide down from this summit, as the ADR model is applied to specific cases, or an ascent as the ADR

approximation is derived and its limitations are better understood. The 1997 compilation edited by *Tilman and Kareiva* gives a good overview of both these endeavours. In this review we will admire some scenery on the climb-up to the ADR approximation by describing a maximally simplified model—the Brownian bug process.

Ocean ecology is a natural setting for ADR descriptions because the spatial domain is large and the populations of some species are enormous. Population size matters because C in (1) is an average or expectation. The actual number of organisms in dA , say N , is a random variable and using the definition in (1) $\bar{N} = C dA$. The difference $N' = N - \bar{N}$ is a *fluctuation*. Deterministic ADR equations ignore these fluctuations. The naive justification for discarding fluctuations is that N is a Poisson random variable (e.g., *Durrett and Levin* 1994) so that

$$\frac{N'}{\bar{N}} \sim \frac{1}{\sqrt{\bar{N}}} \ll 1. \quad (3)$$

Thus a deterministic description like (2) may be useful for copepods, but not for whales.

In oceanography, ADR models are a main line of communication between physicists and biologists. Physical oceanographers put the A into the ADR equation (2) by adding the term $\mathbf{u} \cdot \nabla C$ to the left hand side. The ve-

¹In this note I will work in two-dimensions so that in (1) I am using a control area rather than a control volume.

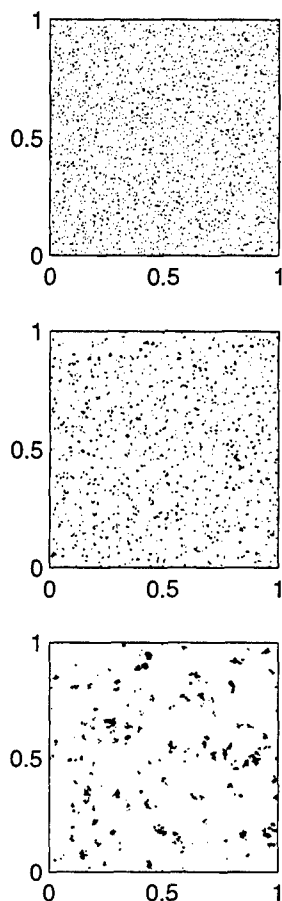


Figure 1. A Brownian bug simulation using $\Delta = 0.001$, $p = q = 1/4$, $N_0 = 4000$, and $U = 0$ (no advection). The position of each bug is plotted as a point in the unit square. The top panel shows the initial condition, the middle panel is after 10 cycles and the bottom after 100 cycles.

locity $\mathbf{u}(\mathbf{x}, t)$ is supplied by some physical model. (For example, see the paper by Kelvin Richards in these proceedings.) Physicists find this type of model appealing because the mathematical structure is familiar, and because it is easy to plug biology into existing ocean models. This is also my excuse for discussing these issues in a meeting devoted to oceanographic stirring and mixing.

When I described the Brownian bug process in my presentation at the 2001 'Aha Huliko'a meeting, Mel Briscoe pointed out that the same model had been independently presented at the 1997 'Aha Huliko'a meeting by Robert Adler and identified as a *superprocess*. Adler approaches this subject from the perspective of

a probabilist and the references in his article provide an entry into the extensive and very mathematical literature on superprocesses. A Google search on "superprocess" gives about 250 hits, most of which are on the homepages of mathematicians. Table stakes in the superprocess community are an understanding of measure theory and branching processes—most oceanographers can't ante.

Another closely related class of problems is diffusion-limited reactions, e.g., see the review by *Mattis and Glasser* (1998), which emphasizes the utility of quantum field theory in these problems. There seems to be little communication between physicists interested in diffusion-limited reactions and probabilists studying superprocesses.

Ecologists and oceanographers will not find it easy to understand the review articles written by either of these communities. This review, which is intended for my oceanographic colleagues, might then be titled "Superprocesses for pedestrians, with no quantum field theory and no measure theory."

2. Brownian bug simulations

The Brownian bug process is an ensemble of random walkers (idealized as points) milling around in continuous time and space and simultaneously reproducing and dying at constant mean rates. Reproduction is random in time and occurs via binary division, so that parent and progeny are at the same point for just an instant before their independent random walks start to produce \sqrt{Dt} separation. Death is also random and dead bugs are removed from the ensemble. The addition of advection to this scenario (*Young* 2001) results in the simplest model of a planktonic species reproducing and dying in a turbulent fluid.

To simulate the continuous process described above on a computer one must discretize. There are several ways of doing this, and I describe in the appendix an individual-based Monte Carlo procedure which produces Figure 1. The top panel shows the homogeneous initial condition and the middle and bottom panels the results after 10 and 100 cycles of birth, death and diffusion. Patches of bugs spontaneously form out of the spatially uniform initial conditions.

Failure of deterministic ADR. The ADR approximation of the simulation in Figure 1 is simply

$$C_t = D\nabla^2 C + (\lambda - \mu)C, \quad (4)$$

where D is the diffusivity, λ is birth rate, and μ the death rate. (For the relation between D , λ , and μ and the parameters in the simulation see the appendix.) But in Figure 1 birth and death are equiprobable, $\lambda = \mu$,

and consequently (4) collapses to the diffusion equation. Thus, with the initial condition $C(\mathbf{x}, 0) = N_0/L^2$, the solution of the ADR description is $C(\mathbf{x}, t) = N_0/L^2$. Uniform concentration is not a good characterization of Figure 1 and we conclude that the ADR approximation fails to describe the Brownian bug process.

A stochastic ADR equation. Although deterministic ADR fails, there is a stochastic partial differential equation model which does capture the fluctuations exhibited by the individual-based model. This stochastic equation is something like

$$C_t = D\nabla^2 C + \sqrt{C} w(\mathbf{x}, t) \quad (5)$$

where w is a white Gaussian noise. The \sqrt{C} in (5) occurs because in the control volume d the stochastic imbalance between births and deaths is proportional to \sqrt{C} . I qualified the introduction of (5) with "something like" because mathematicians (e.g., Adler 1997) tell us that (5) makes sense only in one dimension, $d = 1$, but not when $d \geq 2$: in that case the concentration $C(\mathbf{x}, t)$ cannot be defined. I do not fully understand this point. In any event, Adler proceeds to introduce an integrated version of (5) which he claims is sensible even in $d \geq 2$. We press on...

Density fluctuations. The spatial clumping in Figure 1 occurs because birth is always next to a living bug, while death can occur anywhere. Alternatively, in some regions because of bad luck there is local extinction of the bug population. Diffusion from the surviving centers of population is not fast enough to recolonize the voids. This suggests that to produce patches the diffusion D must be weak relative to the growth rate $\lambda = \mu$. We can identify the nondimensional parameter that controls this transition by noting that the initial separation distance between bugs (the "specific" length) is $\ell_s = L/\sqrt{N_0}$. On the other hand, using the diffusivity D and the growth rate λ , we can define a "reproductive" length $\ell_r \equiv \sqrt{D/\lambda}$, which measures the separation that develops between parent and progeny before there is another reproductive event. We expect that patchiness will be strong if the nondimensional number

$$\frac{\ell_s}{\ell_r} = L\sqrt{\frac{\lambda}{N_0 D}}, \quad (6)$$

is large. If the ratio ℓ_s/ℓ_r is small then density fluctuations should be small because the diffusion will be effective at mixing a family into the background of unrelated, and therefore uncorrelated, bugs.

To illustrate these considerations, the $L \times L$ square is divided, like a chessboard, into smaller squares ("boxes"), each of size

$$\ell_p \equiv 2^{-p} L. \quad (7)$$

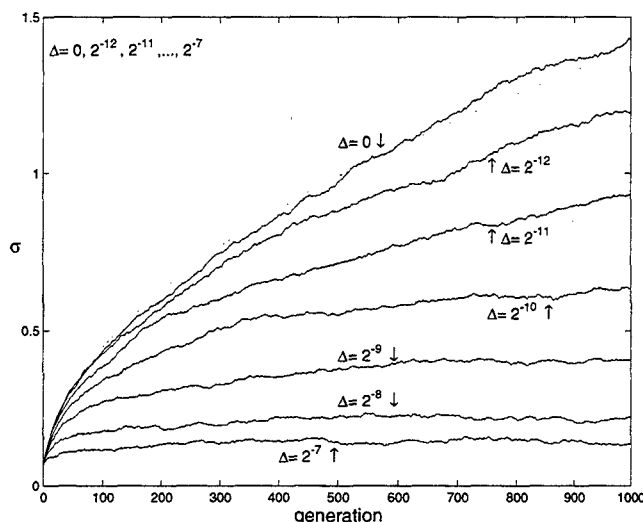


Figure 2. Results of 7 simulations each with $N_0 = 2^{18}$ bugs at $t = 0$. The unit square is divided into a lattice of 32×32 boxes (i.e., $p = 5$) and $\sigma(5, t)$ defined in (10) is computed. The parameters in section 5 are $p = q = 1/4$ and the step-length of the random walk, Δ , is varied as indicated. When the diffusion is strong σ remains close to its initial Poisson value, $\sigma(5, 0) \approx 1/16$. The dotted curve is $\sigma_{GW} \equiv \sqrt{(1 + 2\mu t)/n_p}$, which is computed using the Galton-Watson solution in (18) and (19) below.

There are 2^{2p} boxes so that the expected number of bugs per box is

$$n_p \equiv 2^{-2p} N_0. \quad (8)$$

The occupation number of box b is the fluctuating quantity

$$n_b(t) \equiv \text{the number of bugs in box } b \text{ at } t, \quad (9)$$

where $b = 1, \dots, 2^{2p}$ indexes the boxes. To measure the size of fluctuations in n_b relative to the expected value n_p we use the ratio of the RMS value of $n(b, t)$ to n_p :

$$\sigma(p, t) \equiv \sqrt{\frac{1}{2^{2p}} \sum_{b=1}^{2^{2p}} [n(b, t) - n_p]^2 / n_p}. \quad (10)$$

If $\sigma(p, t) \ll 1$ then $n(b, t)$ is fluctuating weakly around the expected value n_p .

Figure 2 shows $\sigma(p, t)$ for a set of simulations with various diffusivities and $p = 5$. The $\sigma(p, 0)$ is small because the box size $\ell_p = 1/32$ is much greater than the specific length, $\ell_s = 1/512$. If the diffusivity is strong enough (for example, $\Delta > 2^{-8}$ in Figure 2) then $\sigma(p, t)$ experiences mild growth but $\sigma(p, \infty) \ll 1$. In this case the diffusivity is arresting reproductively driven fluctuations. On the other hand, if the diffusion is small then the growth of σ proceeds till $\sigma(p, \infty) \geq O(1)$, which

indicates large fluctuations in the density defined using the box-scale ℓ_p . In particular, if there is no diffusion ($\Delta = 0$) then one can show using the Galton-Watson solution in (18) and (19) that $\sigma(p, t) \approx \sqrt{(1 + 2\mu t)/n_p}$. Notice that by decreasing the diffusivity we are increasing the nondimensional parameter in (6).

It would be useful to be able to give a scaling law for the saturated value, $\sigma(p, \infty)$, in terms of D , μ , ℓ_p and the other external parameters. I have not been able to achieve this.

3. Galton-Watsonology

The Brownian bug model combines two classical stochastic processes: Brownian motion and a Galton-Watson branching process. Brownian motion is familiar to most oceanographers, but the Galton-Watson process is not. This section summarizes some basic properties of Galton-Watson process.

Suppose that we switch off the motion of the bugs, i.e., we set the step length of the random walk to zero. In this case each bug founds a family which sits at the initial spatial location. Newly born bugs pile up and build a tower on top of their ancestors. The towers go up and down as bugs are born and die. Towers can disappear forever (extinction) if a run of bad luck wipes out the family. The statistics of these families, particularly the probability of extinction, were studied by Galton and Watson in the nineteenth century (see *Harris*, 1963, and chapter XVII of *Feller*, 1968). In this review we closely follow Feller's continuous-time formulation of the Galton-Watson process.

The fundamental variables of the Galton-Watson process are the probabilities

$p_k(t)$ = the probability that there are k bugs at t .

We study the proliferation of a family descended from a single urbug using the initial condition $p_1(0) = 1$ and $p_k(0) = 0$ if $k \neq 1$. The probability that a family is extinct at t is $p_0(t)$. Given $p_k(t)$, one calculates the average of a function of k according to the definition

$$\bar{f}(k, t) \equiv \sum_{k=0}^{\infty} f(k, t) p_k(t). \quad (11)$$

Normalization of probabilities requires $\bar{1} = 1$ and the mean population of a family is $\bar{k}(t)$.

The family becomes extinct when a family with one surviving member suffers a death; accordingly the probability of extinction p_0 increases like

$$\dot{p}_0 = \mu p_1. \quad (12)$$

The evolution of the other probabilities with $k \geq 1$ is obtained from the hierarchy of differential equations

$$\dot{p}_k = \lambda(k-1)p_{k-1} - (\lambda + \mu)kp_k + \mu(k+1)p_{k+1}. \quad (13)$$

The term $-(\lambda + \mu)kp_k$ on the right hand side of (13) appears because a family of k bugs might make a transition to $k+1$ bugs if any of its k members reproduce (probability per time λk) or make a transition to $k-1$ bugs if any of the k members die (probability per time μk). Analogous reasoning is used to deduce the other terms containing $k-1$ and $k+1$ on the right hand side of (12).

Mean and variance. From (12) and (13) one can show using the definition (11) that $\dot{\bar{1}} = 1$ and

$$\frac{d\bar{k}}{dt} = (\lambda - \mu)\bar{k}. \quad (14)$$

This result establishes the connection between the Galton-Watson process and the ADR equation (3): both \bar{k} and C are expectations defined by ensemble averages and $\lambda - \mu$ is the growth rate of the expected population. In fact, if we start with N_0 bugs, each of which is a family with one member, then because the evolution is independent $\int C dA = N_0 \bar{k}$.

The statistic \bar{k} contains no information concerning the fluctuations in population. That is, at times $t > 0$ some families are extinct, while others are very large. A coarse description of these fluctuations is provided by the variance $\bar{k}^2 - \bar{k}^2$, or better by the ratio

$$v = \sqrt{\bar{k}^2 - \bar{k}^2}/\bar{k}, \quad (15)$$

which, like (3), compares the fluctuations to the mean.

Assiduous summation of (12) and (13) shows that

$$\frac{d\bar{k}^2}{dt} = 2(\lambda - \mu)\bar{k}^2 + (\lambda + \mu)\bar{k}. \quad (16)$$

If the death rate balances the birth rate, so that $\lambda = \mu$ and $\bar{k} = 1$, then the solution of (16) is

$$\bar{k}^2 = 1 + 2\mu t, \quad (\lambda = \mu). \quad (17)$$

In this case $v = \sqrt{2\mu t}$, indicating that the system is dominated by fluctuations as $t \rightarrow \infty$.

The special case $\lambda = \mu$ in (17) is the critical point of the branching process. If $\gamma \equiv \lambda - \mu > 0$ then $\bar{k} \sim \exp(\gamma t) \rightarrow \infty$ and $v \sim \exp(-\gamma t/2) \rightarrow 0$. On the other hand, if $\gamma < 0$ then $v \sim \exp(-\gamma t/2) \rightarrow \infty$. The conclusion is that the system is dominated by fluctuations if the growth rate γ is less than or equal to zero.

A solution with $\lambda = \mu$. The variance is only a rough guide to behaviour of fluctuations. A much more informative result is provided by an explicit solution of (12) and (13) which is obtained using the generating function method (Feller 1968):

$$p_0(t) = \frac{\mu t}{1 + \mu t}, \quad (18)$$

and if $k \geq 1$:

$$p_k(t) = \frac{(\mu t)^{k-1}}{(1 + \mu t)^{k+1}}. \quad (19)$$

At large times, $\mu t \gg 1$, see that most families are extinct, $p_0(t) \rightarrow 1$. That is, at large times the *most probable* number of members in any given family is zero — in fact extinction is certain. On the other hand $k = 1$ so that the expected number of members in a family (counting extinct families as having zero members) is always constant.

To reconcile the extinction of most families with a constant expected population, we make a distinction between surviving families (meaning a family with at least one member) and extinct families. Suppose that we start with a large number $N_0 \gg 1$ of individuals, each of which founds a family. At t the number of surviving families is a random variable, $F(t)$. The expected number of surviving families is $\bar{F} = (1 - p_0)N_0$, or using (18)

$$\bar{F}(t) = \frac{N_0}{1 + \mu t}. \quad (20)$$

Let the random variable n be the number of individuals in a surviving family. From (18) and (19), the probability distribution of n , conditioned on the survival of a family, is

$$p_n = \frac{(\mu t)^{n-1}}{(1 + \mu t)^n}, \quad (n = 1, 2, \dots). \quad (21)$$

and consequently

$$\bar{n}(t) = \mu t + 1, \quad \bar{n}^2 = (2\mu t + 1)(\mu t + 1). \quad (22)$$

Thus, the number of surviving families decreases like t^{-1} , while the membership of a surviving family grows like t^1 to keep the total population fixed.

These remarks illustrate Galton and Watson's conclusion that the "observed diminution of surnames among families whose history we can trace, is not a sign of their diminished fertility." Instead the extinction of most families, and the apparent fecundity of a few exceptions, is a result of "the ordinary law of chances."

4. Spectral dynamics

We began section 3 by imagining that the bugs were immobile so that the surviving families formed towers on top of the urbug. We then ignored the spatial aspects of the model, and focussed simply on the statistics of the bug population. Now let us return to the spatial domain and study the spectrum of concentration fluctuations.

For the moment, we continue to assume that the bugs are immobile ($D = 0$). The discussion surrounding (20) through (22) shows that the height of a typical family tower grows like $1 + \mu t$ and the average separation between towers grows like $\ell_s/\sqrt{1 + \mu t}$, where $\ell_s \equiv L/\sqrt{N_0}$. We can write the microscopic density of bugs in a single realization of the process as

$$\rho(\mathbf{x}, t) = \sum_{f=1}^F n_f \delta(\mathbf{x} - \mathbf{x}_f), \quad (23)$$

where $F(t)$ is the number of surviving families, n_f is the number of members in family f and \mathbf{x}_f is the location of the family. Notice that the concentration is

$$C = \langle \rho \rangle = N_0/L^2, \quad (24)$$

where the $\langle \rangle$ denotes an ensemble average over the random locations \mathbf{x}_f and an average over the n_f 's using (21). The average $C = \langle \rho \rangle$ is trivial — just like \bar{k} in the previous section. To learn something about the fluctuations we must study quadratic quantities such as the spectrum.

Continuing with the $D = 0$ assumption, we now make a standard calculation of the spectrum by ensemble averaging the density in (23). The Fourier series representation of (23) is

$$\rho(\mathbf{x}, t) = L^{-2} \sum_{\mathbf{k}} \rho_{\mathbf{k}} \exp(i\mathbf{k} \cdot \mathbf{x}), \quad (25)$$

where

$$\rho_{\mathbf{k}} = \sum_{f=1}^F n_f \exp(-i\mathbf{k} \cdot \mathbf{x}_f). \quad (26)$$

The spectrum is related to

$$\langle \rho_{\mathbf{k}} \rho_{\mathbf{k}}^* \rangle = \left\langle \sum_{f=1}^F n_f^2 + 2 \sum_{f' > f} n_f n_{f'} e^{i\mathbf{k} \cdot (\mathbf{x}_{f'} - \mathbf{x}_f)} \right\rangle, \quad (27)$$

where the $\langle \rangle$ is an ensemble average over both the random and uncorrelated positions \mathbf{x}_f of the surviving families and over the random variable n_f . Because there are

²The family locations \mathbf{x}_f are uniformly distributed in the domain. Thus $\langle \delta(\mathbf{x} - \mathbf{x}_f) \rangle = L^{-2}$ and if $\mathbf{k} \neq 0$ then $\langle \exp(i\mathbf{k} \cdot \mathbf{x}_f) \rangle = 0$.

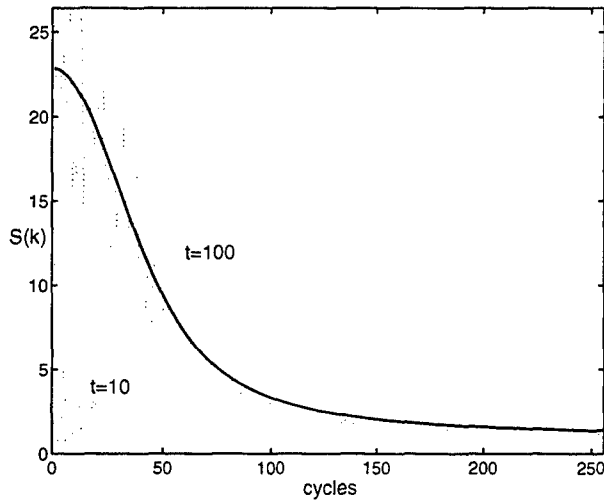


Figure 3. Comparison of the analytic prediction (31) (the smooth solid curve) with the results of simulation. We show estimated spectra (the three dotted curves) from the simulation at $t = 1$, $t = 10$ and $t = 100$; the comparison with (31) is made only at $t = 100$. The simulation used $N_0 = 10^5$ bugs with $\Delta = 2^{-11}$ and $p = q = 7/64$. The spectra are estimated by azimuthally averaging in the wavenumber plane.

no correlations between the positions of the families the final term, involving the double sum with $f \neq f'$ vanishes. Using \bar{F} from (20), and \bar{n}^2 from (22), shows that the remaining term on the right hand side of (27) is

$$\langle \rho_{\mathbf{k}} \rho_{\mathbf{k}}^* \rangle = \bar{F} \bar{n}^2 = N_0(1 + 2\mu t). \quad (28)$$

This simple calculation indicates that the spatial signal of a diffusionless Galton-Watson process is a white spectrum which rises at a constant rate.

How is the conclusion above affected by diffusion? With $D \neq 0$ the members of a family move as independent random walkers and the family towers blur into spreading clouds of bugs. We could write down a microscopic density, analogous to (23), in which the position of each individual bug is represented with a δ -function. But then the calculation founders at (27) because the $\langle \rangle$ no longer kills the off-diagonal terms: there are correlations between the positions of bugs which belong to the same family. Instead we can argue heuristically that the evolution of the spectrum, defined as

$$S(k, t) \equiv N_0^{-1} \langle \rho_{\mathbf{k}} \rho_{\mathbf{k}}^* \rangle, \quad (29)$$

is given by

$$S_t = 2\mu - 2Dk^2 S, \quad S(k, 0) = 1, \quad (30)$$

where $k \equiv \sqrt{\mathbf{k} \cdot \mathbf{k}}$. The first term on the right hand side of (30) is a source of variance which produces the uniform rise of the spectral level in (28). The final

term is the diffusive sink of variance which ultimately balances the source.

The solution of (30)

$$S(k, t) = \frac{\mu}{Dk^2} (1 - e^{-2Dk^2 t}) + 1, \quad (31)$$

exhibits a k^{-2} range at high wavenumbers. (If we isotropize by using $2\pi k S(k)$ then this is a k^{-1} spectrum.) Figure 3 shows good comparison of (31) with a spectrum estimated from a simulation.

5. Conclusions

In this note we have studied a model which focuses attention on the role of fluctuations in the spatial development of populations. It is remarkable that Euler, Navier and Stokes formulated the basic equations of fluid mechanics before the reality of atoms was established. This history indicates that for most purposes atomic fluctuations are unimportant in fluid mechanics. The Brownian bug model suggests that the problem of biological fluctuations is more severe, and that events on microscopic scales can impact macroscopic observations. Indeed, the source term 2μ on the right hand side of (30) is due to reproduction and has no analog in fluid mechanics.

Appendix: A recipe for simulations

The initial condition, $t = 0$, is prepared with a large number N_0 of bugs, strewn randomly into an $L \times L$ square domain. The initial condition is a Poisson point process in which there are no correlations between the positions of the bugs.

The simulation is advanced through time in increments of a "cycle" of duration τ . Each cycle consists of two steps: (a) random birth and death; (b) Brownian motion. In step (a) each bug reproduces by binary fission (probability p) or dies (probability q) or remains unchanged (probability $1 - p - q$). When a lucky bug divides the offspring is placed on top of the parent. In step (b), bug k is displaced to a new position $\mathbf{x}_k(t + \tau) = \mathbf{x}_k(t) + \delta \mathbf{x}_k(t)$. The components of $\delta \mathbf{x}_k$ are independent and identically distributed Gaussian random variables, each with RMS value Δ (i.e., Brownian motion with the diffusivity $D = \Delta^2/2\tau$). These independent displacements separate the coincident parent-progeny pairs created by step (a).

In principle, one can approach the continuous limit by taking $\tau \rightarrow 0$ while holding the parameters $\lambda \equiv p/\tau$, $\mu \equiv q/\tau$, and $D \equiv \Delta^2/2\tau$ fixed.

We can also use $p_0(t)$ in (18) to calculate the probability that an initial population of N_0 bugs becomes extinct at time t : each bug produces a family which

evolves independently of the other families, so that the probability that all N_0 families are extinct at t is

$$p_{\text{ext}} = p_0^{N_0} \approx \exp(-T_{\text{ext}}/t), \quad (\text{A1})$$

where the extinction time-scale is $T_{\text{ext}} \equiv N_0/\mu$. (The exponential approximation in (A1) assumes that N_0 is large and t/T_{ext} is of order unity.) In simulations we avoid extinction by making N_0 much larger than the number of generations. The suppression of extinction is a consequence of approaching the "thermodynamic limit" in which $N_0 \rightarrow \infty$ with N_0/L^2 fixed.

Acknowledgments. I am grateful to many people for discussions of this problem. My research is supported by the National Science Foundation, most recently by NSF OCE96-16017.

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This preprint was prepared with AGU's L^AT_EX macros v4, with the extension package 'AGU++' by P. W. Daly, version 1.6a from 1999/05/21.